

PAPERS.

1. Distant Orientation in Amphibia.

By BRUCE F. CUMMINGS*.

[Received September 1, 1911 : Read October 24, 1911.]

(Text-figures 4 & 5.)

INTRODUCTION.

The observations and experiments detailed below were made in North Devonshire during the course of the last two years. The Amphibia chiefly used were two species of Newts. The British Newts have a peculiar geographical distribution in these Islands, and, living in the north of Devon, I was fortunate in being able to obtain large quantities of two species, *Molge cristata* Laur., and *Molge palmata* Schneid. It has long been the custom of field naturalists, year after year with all the precision of Gilbert White of Selborne, to note the date of the first return of Frogs and Efts to their breeding-ponds as indicative of the return of spring. It occurred to me to enquire how the Amphibia find the water again after having left it in the autumn of the preceding year. Nothing appears to be known of this subject, although the problem of these amphibian migrations is a simple one compared with that of the migrations of birds, which has attracted, and still is attracting, so much attention from the students of animal life. No one has shown how the Amphibia find the water, and it is not definitely known whether the Amphibia return to the same piece of water each spring, nor whether every animal or only a lucky small percentage finds water as the breeding season comes round, nor precisely how extensive their perambulations on land may be during the autumn months before hibernation sets in. Many larval Newts, and a few adult Newts of *Molge palmata* remain in the water hibernating at the bottom of the pond. But these are exceptional. The majority of our Amphibia do leave the water, and large numbers annually find their way back to it in the following spring. The Newt is essentially a nocturnal animal, and a visit to a newt-pond with a lantern after dark, whether in spring or autumn, is sufficient to show that night is the time when the migrations are carried on. The answer to the question how these amphibian migrations are performed must involve points of importance to amphibian psychology and, when elucidated, the subject will form an interesting chapter in their natural history. The literature is scant and vague. G. J. Romanes† thought that Frogs had a distinct idea of locality. He based this idea on the cases reported to him by some of his correspondents, where Frogs, removed a distance of 200 or 300

* Communicated by T. A. COWARD, F.Z.S.

† G. J. Romanes, 'Animal Intelligence,' p. 251.

yards from their habitual haunts, returned to them again and again. He also expressed the opinion that Frogs were able to perceive moisture from a great distance, and he quotes Warden who in "An Account of the United States," vol. ii. p. 9, says that a pond containing some Frogs having dried up, the animals "made straight for" the nearest water, though it was eight kilometres away.

COMPENSATORY HEAD-MOVEMENTS.

In all experiments with the Amphibia it is necessary to beware of error through compensatory head-movements, which, if neglected, give a false complexion to the results. No mention of them is made by Romanes' correspondents and no details of the experiments are given. It is astonishing to find how persistently Newts will return and immediately re-enter their pond, after they have been removed from it to some considerable distance. Even when placed heading directly away from the water, they turn round and walk towards the water, as if endowed with a quite uncanny knowledge of the geographical features of the neighbourhood of their breeding-pond. The explanation partly lies in the head-movements contrary to the movement of rotation, set up by the motion of the experimenter's hand as he turns the Newt round to face away from the water. The Newt mechanically responds by turning round, with the head towards the water. These movements are very pronounced in the Newt on account of its linear shape. A Newt, on a rotating disc which is being moved backwards and forwards through an angle of 180° , responds correctly if the motion is slow, *i. e.*, it turns its head regularly in the opposite direction to the backward and forward movements of the disc. If the motion of the disc be fast, it overtakes the slow head-movements of the Newt, and the Newt becomes confused and escapes from the predicament by lowering its chin so as to place it in contact with the moving disc. No response is then given. Continuous rotation in one direction produces no very marked external signs of giddiness. But in the Common Toad (*Bufo vulgaris*) these signs are marked. While the disc is moving the head is motionless. As soon as it stops, the Toad begins to crawl round in circles moving in the direction the disc had been moving. One of these animals, after rotation of one minute, in this way crawled through four circles! If a Newt be rotated through 90° in a trough with perpendicular walls two inches high, I have seen it turn in response to the rotation and climb over the side.

GEOTAXIS.

This subject must also be taken into consideration. It must be borne in mind that the ground around most ponds is sloping. Most fresh water lies at the bottom of hollows or at the foot of slopes. Newts are positively geotactic. They preferred to walk

downhill when I tested them in the spring, but in the autumn this preference changed and they went up. In work with an inclined plane, *Molge cristata* was chiefly used. The Newts were kept in water in large earthenware pans under similar conditions so far as possible. The observations were made in the early morning or at night, always in subdued light. The plane was of wood and measured 125 centimetres by 82 centimetres 5 millimetres. A line was drawn transversely across the plane, and each Newt on removal from the pan was allowed to crawl on a level surface adjoining until manœuvred with the finger into the right direction, when it was swiftly lifted on to the incline and left in a horizontal position. In this way I cut out errors arising from compensatory head-movements. An interval of ten minutes was allowed each animal before being tried again. This prevented errors arising from simple habit formation, which in the Newt is rapid.

Table I. shows the results of experiments performed in the spring when the Newts, used singly, walked downhill in 80 per cent. of the tests. Similar results were obtained by using Newts in series; twenty Newts were used. The number of positive responses was in this way reduced to 67 per cent., which perhaps is nearer the truth. Table II. was obtained in the autumn when the Newts were endeavouring to leave the water for winter quarters. The Newts were then negative and walked uphill 72 per cent. of the times. In this table the Newts were used in series, the first row being worked by twenty *Palmates* and the rest by twenty *Crested*.

TABLE I.

No. of Newt.	Incline.	Position at Start.	Down.	Up.	Neutral.	Total.
1	16°	Horizontal.	12	0	0	12
1	16°	Facing Up.	1	0	0	1
1	12°	Horizontal.	11	1	0	12
2	10°	„	10	1	1	12
2	10°	Facing Up.	2	1	0	3
3	10°	Horizontal.	12	2	1	15
3	10°	„	6	1	0	7
4	5°	„	10	1	3	14
4	5°	Facing Up.	3	0	0	3
4	5°	Horizontal.	7	3	3	13
Totals			74	10	8	92

TABLE II.

Incline.	Position.	Down.	Up.	Neutral.	Total.
8°	Horizontal.	4	19	1	24
8°	"	8	33	0	41
8°	"	13	26	4	43
Totals		25	78	5	108

The real cause of the Newts normally walking downhill may lie in the weakness of the limbs. Yet, from a few observations made on the strong-limbed Toad placed horizontally on an incline, I am induced to think that it also usually goes down, if given the choice. But, as in the case of the Newt, the cause of this behaviour of the Toad when placed *horizontally* on an incline receives a simple mechanical explanation. The kick given by the hind leg, which is higher up the incline than the other, would naturally tend at the moment of the hop to turn the animal downwards. The Toad always *hops* downhill, but it crawls and rarely *hops* up a gradient. On an incline of 12° one of my Toads would begin hopping downhill. If it was then teased on one side so as to send it up, the Toad would endeavour to continue hopping uphill, but when once facing up, the gait very quickly changed to a crawl. It may be observed that when endeavouring to hop up, the hind limbs cannot be brought up under the body from a state of extension unless they scrape the ground. After they have once scraped the ground in this way, the Toad ceases to attempt to hop, but crawls. It would appear, therefore, antecedently probable that in the spring, at the time of their greatest activity, the general tendency of the Toad also would be downhill towards water, rather than up.

One more observation is worth recording. Some Newts, when placed on a level surface or on only a slight incline, would never start off straight in any direction. They always turned, and some of their turns were very elaborate. They would meander about the centre of the board around and up and down, before setting out in any particular direction. When once started, however, they went ahead. I regard this elaborate turning merely as a complex withdrawing response. Similar behaviour has been noted in the Crayfish*.

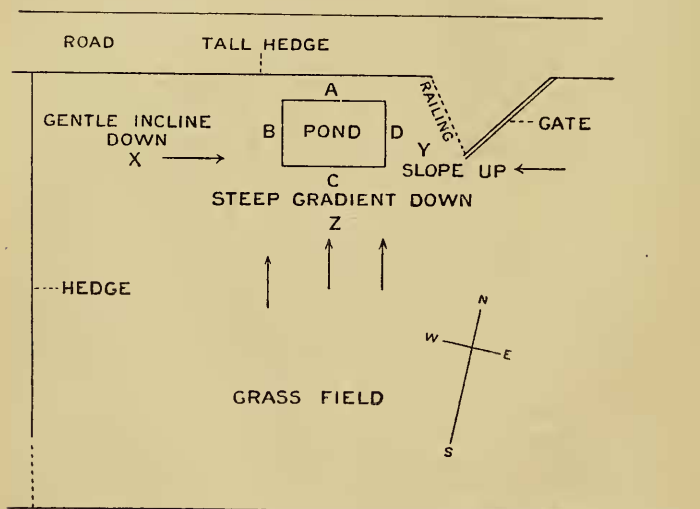
All those Newts which winter on the slopes around the pond could, by their geotactic responses, easily find their way back to the water in spring. They would simply walk downhill.

* J. Carlton Bell, "Reactions of the Crayfish," Harvard Psychological Studies, Vol. ii. 1906, p. 615.

HOMING EXPERIMENTS, 1910.

The first step was to find a pond suitable for experimental purposes, which was not easy in this neighbourhood where ponds are not common. Eventually I found a pond, which though not by any means the best possible, yet fulfilled sufficiently the required conditions. It was conveniently near home, it contained a good number of Palmate Newts, and was small enough to admit of a thorough dredging. Text-fig. 4 represents the general nature of the surroundings. The sides of the pond were bricked up, and there was a thick sediment of mud at the bottom. The three sides A, B, C, rose perpendicular from the water for a foot, while at the fourth and remaining side the water was level with the edge. The depth was 18 inches on an average, but it varied of course at different states of the weather and at different periods of the spring season. The area of the surface-water exposed was 4 sq. metres 60 sq. decimetres.

Text-fig. 4.



Plan showing pond and its surroundings used for homing experiments
Nos. 1-10.

The pool occupied a very sheltered position and was protected from all winds except those from an easterly direction. For dredging the pool I used a large prawning net on a long pole. At first I could not be sure that the pool was efficiently dredged, as it was impossible to see whether all Newts had been satisfactorily removed. Subsequently I was in several ways able to show that the pool could be thoroughly cleared, when necessary, of all Newts, if the dredging was carefully done.

In the experiments the method was to collect a number of Palmate Newts, mark them and set them loose near the pool at different distances from it. Each separate batch of Newts was given its own special mark, so that the animals when recovered could be immediately assigned to their respective batches. After several unsuccessful attempts at ringing with fine aluminium wire, I came to the conclusion that the simplest and best way of marking them was by amputating the toes of the feet in a variety of combinations.

The toe was snipped off close to the base with a pair of fine scissors. In the case of some controls, operated on and kept in an observation-pan, these animals could be easily distinguished from unmarked ones even after the lapse of two months, and this period of time for the purpose of the experiments was ample, so that I had nothing to fear from regeneration. Two days after the operation, the Newts were set loose at nightfall on the ground near the pool. They were always placed heading towards the pool, and care was taken not to influence the immediate course of the Newts through the reactions of compensatory head-movements.

Experiment 1. In this experiment twenty-one Newts were collected from a large pond 10 miles away from the experimental pond. This collection was divided into three lots of seven each, and each batch bore its distinguishing mark. On April 26th:—

Batch A was placed 15 yards from the edge of the pool on the incline X.

Batch B was placed „ „ „ „ „ on the incline Y.

Batch C was placed 10 yards up the steep slope Z.

Result. Next morning none of the marked Newts had succeeded in finding the water. On April 29th one of Batch C was recovered, and one of Batch B on the following day. On May 13th one of Batch A was taken. Thus only three were recovered.

Experiment 2. A collection of twelve Newts was made from the pond 10 miles away, marked and treated as usual. On May 8th six were placed 5 yards away at Y, and six 10 yards away at Z. These two lots were marked distinguishably one from another and from all other lots, as in all other experiments with one exception.

Result. Next day none had found the water. No signs of them on May 14th. On May 29th one, the only successful animal, was obtained. It was one of the Batch at Z.

Experiment 3. Seven more marked and imported Newts were placed at X, 5 yards from the pool, on May 26th. One was recovered on May 29th.

Recorded below are the experiments with Newts collected from the experimental pool itself and set free in its precincts after the usual treatment.

Experiment 4. Fourteen Newts were collected and on April 30th seven were placed 10 yards away at Z, and seven 5 yards away at Y.

Result. No Newts had returned by the next day, but seven were recovered on May 4th and four more on May 14th, making 11 out of the 14. In this experiment I did not take the precaution of making the two lots distinguishable when marking them, so that I could not refer the animals recovered to their respective batches.

Experiment 5. Six natives were collected and set loose on May 12th, 10 yards away at Z.

Result. None had returned on the 13th, three were recovered on the 14th. On May 29th the fourth returned, and on June 1st the fifth was taken.

Experiment 6. On May 30th six natives were placed at X, 5 yards from the pool.

Result. On June 1st five were recovered.

After this date the approach of summer weather made further work for the year prejudicial to reliable results.

HOMING EXPERIMENTS, 1911.

I took the precaution of beginning earlier in the spring this year, and the following few experiments which I was able to carry out shew that a greater proportion of imported Newts was recovered.

Experiment 7. On March 26th six natives were set loose, 12 yards away from the pool along the incline at X.

Result. Next day none had returned. Two were caught on March 29th, one on March 30th, one more on April 5th, and the fifth, and last to be recovered, on April 9th.

Experiment 8. On April 2nd six natives were set loose along the same incline but 24 yards from the pond.

Result. The next day the only successful animal was recovered.

Resuming with imported Newts, the following experiments were made :—

Experiment 9. On April 2nd six imported Newts were placed 6 yards from the pond, along the incline at X, six more 12 yards away along the same incline.

Result. The next day none had returned. On April 7th one of the 6-yards' lot was obtained and one more on the 12th. Three of the 12-yards' batch were obtained, one on April 5th, one on the 7th, and the third on the 12th.

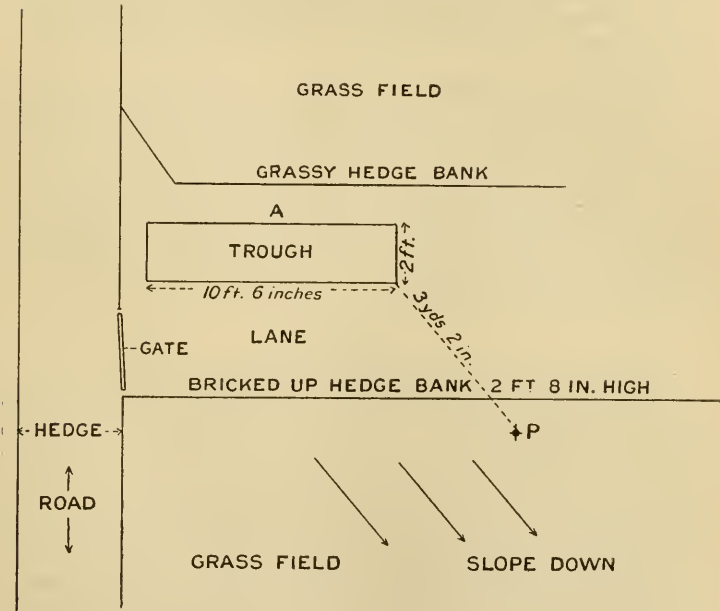
Experiment 10. On April 16th 24 imported Newts were set loose in the neighbourhood of the pond in four Batches :—

- | | | | | | | | | |
|----|---|-------------|---|-------|-------|-----|---------|-------------------|
| A. | 6 | were placed | 5 | yards | along | the | incline | X. |
| B. | 6 | " | " | 12 | " | " | " | X. |
| C. | 6 | " | " | 24 | " | " | " | X. |
| D. | 6 | " | " | 40 | yards | up | the | steep gradient Z. |

Result. On April 18th one of Batch B was caught and two of Batch A. On April 22nd one more of Batch A was obtained.

Experiment 11. In this experiment four full-grown Palmate Newts were taken from a horse-trough about one foot deep near the experimental pond. The trough was only 2 inches above ground level. Text-fig. 5 shows the nature of the ground around this trough and the point (P) at which these four marked Newts were set loose, together with four young Frogs, also caught in the trough, the eight specimens being the whole of the amphibian livestock which the trough contained. The Frogs were young—not more than 10 or 11 months old and hatched the previous spring, judging from their size. These eight specimens were set loose on April 16th.

Text-fig. 5.



Plan showing the horse-trough and its surroundings used for homing experiment No. 11.

The spot where they were set loose was deliberately chosen as the most unfavourable one from which the Newts might be expected to be able to return. They were set heading down the slope away from the trough.

Result. The trough remained empty until May 16th, when one of the four Newts was recovered.

HUMIDITY EXPERIMENTS.

In order directly to test Newts for a supposed faculty for perception of humidity in the atmosphere, I planned apparatus to work with electric fans driving two air currents which were to be kept at an even temperature and velocity. One current was to be thoroughly saturated by passage over a series of porous plates containing water, and the other to be kept dry. The Newt to be tested was to walk down an inclined runway, and to be exposed on one side to the wet current and on the other to the dry. At the bottom of the runway it was free to move in the direction of either current. Fortunately for me, before carrying out this elaborate apparatus in detail, I took the precaution of making a few of what I considered would prove only preliminary trials with a simpler arrangement in which the temperature factor was not eliminated. I quickly formed the opinion either that Newts were unable to detect moisture at a distance and slight variations in temperature, or that my method of experimenting was unsatisfactory.

Although the existence of this faculty—which Romanes favoured—seems improbable in the face of the facts recorded in the two previous sections, an ingenious experimenter might perhaps obtain more encouraging results. I think, though, such a perceptive power in Newts would prove to be of too slight a nature to be easily demonstrated by a laboratory experiment, and especially by one such as mine, where a turn right or left at the end of a runway, after a comparatively short exposure to the conditions, was to decide each test.

DISCUSSION.

The evidence presented, fragmentary as it is, lends support to the hypothesis that Newts and presumably other Amphibia possess a homing faculty. Table III. is interesting, particularly that part dealing with the imported Newts, as one would have been led to expect more of these to return if only by chance; for they were set loose at very short distances from the pond (with one or two exceptions). But then the small size of the pond must be remembered, particularly in comparing with the account in Romanes' 'Animal Intelligence' where no mention of the size of the pond concerned is given. It will be seen that more imported Newts got back in 1911 than in 1910. This may be explained by the fact that experiments in 1911 were begun earlier than in 1910, when the Newts might have already done some breeding before being caught. Their desire to find water would then be proportionately less. This qualification does not apply to the natives, as the same natives were used several times over and their breeding was therefore prevented up to May in both years. Furthermore, in the experiments of 1911, the Newts, both imported and native, were set loose, with one exception, along the incline X. This incline was undoubtedly the most

TABLE III.

(a) *Imported Newts.*

Exp. 1910.	Number set loose.	Position.	Distance in yards from the pool.	Number recovered.
1 ...	7	X	15	2
1 ...	7	Y	15	0
1 ...	7	Z	10	1
2 ...	6	Y	5	0
2 ...	6	Z	10	1
3 ...	7	X	5	1
1911.				
9 ...	6	X	6	2
9 ...	6	X	12	3
10 ...	6	X	6	3
10 ...	6	X	12	1
10 ...	6	X	24	0
10 ...	6	Z	40	0
76				14

(b) *Native Newts.*

Exp. 1910.	Number set loose.	Position.	Distance in yards from the pool.	Number recovered.
4 ...	7	Z	10	} 11
4 ...	7	Y	5	
5 ...	6	Z	10	
6 ...	6	X	5	
1911.				
7 ...	6	X	6	5
8 ...	6	X	24	1
38				27

favourable position for the Newts from which to find the pool. It was a gentle incline down, and they would naturally walk down it. On the other hand, if they turned to the right, they were confronted with the steep gradient Z which in all probability they would not negotiate. The hedge on the left was the only thing which may have lured them away from the right path. In 1910 the number of natives in the pool was twenty-two. In 1911 this supply had fallen to twelve, and two of these still bore marks, sufficiently clear for me to be able to identify them as belonging to batches of native Newts set free the previous year. These two at all events must have wintered near the pool and returned to it in the spring. The decrease in the supply of natives in the spring of 1911 may be explained when I say that seven of the original twenty-two were accidentally killed before they could be returned to the pond at the close of

the 1910 work. It is probable from this that the number in any one pond remains fairly constant. It will be noticed that of the native animals set loose in Experiment 11 only one got back. These were set loose, however, as will be seen in text-fig. 5, in the worst possible position I could find from which the Newts—even natives—might be expected to return. The slope led away down the field from the pond and the field was separated from the trough by a drop of several feet and a hard road three yards across.

A decisive result brought out by these homing experiments is that Newts certainly have no very definite faculty or instinct for detecting water even from a short distance (see Table III.); and in this connection attention may be drawn to the length of time usually taken by the native Newts in finding water from short distances. They perhaps rely on a combination of small clues, for, in addition to the downhill tendency and a small homing faculty, a supposed sensitiveness to atmospheric moisture at a distance and to slight variations in temperature, I can suggest as auxiliary factors (but can adduce no evidence for or against):—a sense of smell for detecting stagnant water and a sense of hearing for discovering other Amphibia already in the water, or, in those Amphibia which live in streams, for discovering running water.

Either all or a few of these may provide the animals with clues, small though some of them would be. In this paper a combination of the downhill tendency and a homing faculty is considered as the chief factor.

I was very anxious to make more experiments with natives, but the stock became exhausted and this brought my work to a premature close.

CONCLUSION.

This paper does not pretend to present a conclusive case on the subject of amphibian migration. But the results of the experiments are suggestive, and the opinions I have formed from them are:—

1. That Newts are helped to find water in which to breed by their marked tendency to walk downhill. Those animals hibernating on the slopes around their pond would simply have to walk downhill. A good many young Newts I have found hibernating in this way, close to the water of their native pond. It may be a wise precaution, because young Newts of the year would not have any knowledge of locality.

2. That there is a small homing faculty in Newts, which probably consists in a topographical knowledge of the locality where the breeding pond is situated.

3. That they are able to “home” from only short distances and that, therefore, both their topographical knowledge and their terrestrial wanderings in autumn and winter must be rather circumscribed.

4. That, speaking generally, the same Newts return to the same pond each year.

5. That those Newts which wander away from the precincts of

the pool, become "lost" and only regain the water by chance or, for a season, may even fail altogether to reach water and to propagate their kind. Field naturalists are well acquainted with the Newt's capacities for travelling.

6. That further experiments on a more extensive scale ought to settle this matter; suitable ponds, however, are difficult to find, particularly in this part of the country.

I hope those living in more favoured localities will be induced to carry these preliminaries to more decisive results.

In conclusion, I should like to thank Dr. R. M. Yerkes, of Harvard University, for the encouragement he has given me in this undertaking, and my sister for her services in obtaining specimens and in dredging.

2. Some Remarks on the Habits of British Frogs and Toads, with reference to Mr. Cummings's recent communication on Distant Orientation in Amphibia. By G. A. BOULENGER, F.R.S., F.Z.S.

[Received November 6, 1911; Read November 21, 1911.]

In the course of the discussion which followed Mr. Cummings's communication at the Meeting on October 24, I made some remarks on the habits of Batrachians, which the Secretary has asked me to embody in a short paper for the information of those who might feel inclined to carry on further observations in this country on the interesting subject with which Mr. Cummings has dealt.

There is great diversity among Tailless Batrachians in the possession, lack, or degree of instinctive foresight in selecting places for the deposition of their eggs. Leaving out the thoroughly aquatic Edible Frog (*Rana esculenta*), which has only doubtful claims to be regarded as British, two of our species, the Common Frog (*Rana temporaria*) and the Natterjack Toad (*Bufo calamita*), belong to the category of the least gifted in this respect, whilst the third, the Common Toad (*Bufo vulgaris*), behaves differently, and is besides possessed of an instinct for orientation which appears to be highly developed. The fact that, after the perfect condition is attained, Tailless Batrachians, unlike the Tailed, do not regenerate lost parts, would render the Common Toad further suitable for experiments on migrations, after the amputation of a finger or toe, as a distinctive mark. The Natterjack is, with us, a very local species, but the Common Toad and the Common Frog are ubiquitous and, as young or outside the breeding-season, are often found far from water, to which they have, of course, to resort for oviposition. How the three species behave in connection with this function I will tell briefly from my own observations.

The COMMON FROG exercises little discrimination in the choice